Statistical structure of neural spiking under non-Poissonian stimulation

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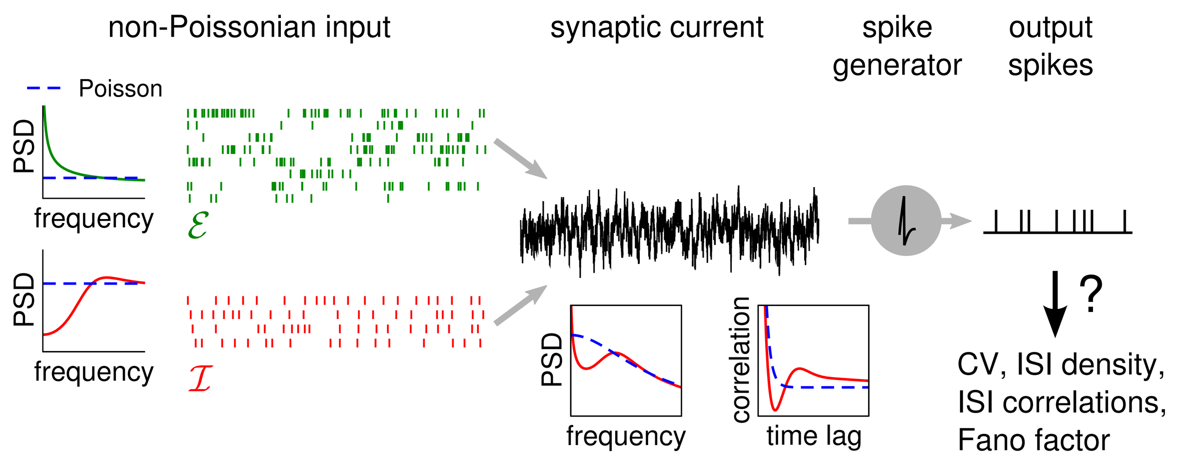
Motivation

- Can we understand the interspike interval (ISI) statistics of spontaneous neural activity?
- What is the relation between input and output statistics of a neuron? --> Important for understanding population activity.
- Most theoretical studies assume that neurons are driven by Poisson spike trains ("white noise" processes, i.e. uncorrelated in time)
- However, realistic synaptic inputs have temporal structure ("colored noise"), e.g. due to refractoriness, bursting, structured "signals", short-term synaptic plasticity, oscillatory activity, adaptation.



Wanted:
Spiking statistics for *arbitrary input correlation function*?

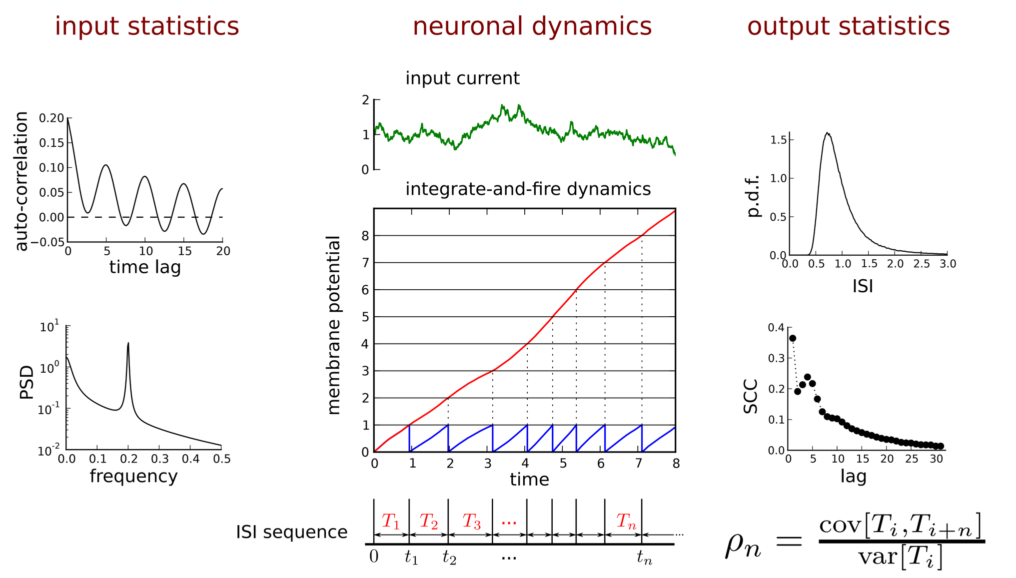
General theory

Perfect integrate-and-fire model

$$C_\mathrm{m}\dot V = I_0 + I_\mathrm{syn}(t), \quad \text{if } V = V_\mathrm{th}: \quad V \to 0.$$

- diffusion approximation: $\dot V = \mu + \sigma\eta(t)$
- noise correlation function $C(t) \equiv \langle \eta(t')\eta(t'+t)\rangle$
- *first-passage problem* for non-Markovian process *V(t)*
- **Trick:** d-dimensional Ornstein-Uhlenbeck process

$$\eta = \mathbf{b}\cdot\mathbf{Y} \qquad \dot{\mathbf{Y}} = \mathbf{A}\mathbf{Y} + \mathbf{B}\boldsymbol{\xi}(t),$$

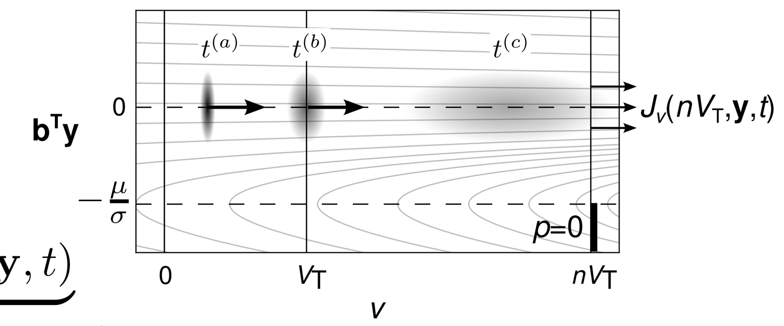


Fokker-Planck equation for $p(v,\mathbf{y},t)$

$$\frac{\partial p}{\partial t} = -(\mu + \sigma\sum_{i=1}^{d} b_i y_i)\frac{\partial p}{\partial v} - \sum_{i,j=1}^{d} A_{ij}\frac{\partial}{\partial y_i}(y_j p) + \sum_{i,j=1}^{d} D_{ij}\frac{\partial^2 p}{\partial y_i \partial y_j}$$

initial condition: $p(v,\mathbf{y},0) = \delta(v)\frac{1+\epsilon\mathbf{b}\cdot\mathbf{y}}{\sqrt{(2\pi)^d|\Sigma|}}\exp\left(-\frac{1}{2}\mathbf{y}^\mathrm{T}\Sigma\mathbf{y}\right)$

n-th-order interval density



$$P_n(t) = \int \mathrm{d}^d y \underbrace{J_v(nV_\mathrm{th},\mathbf{y},t)}_{(\mu+\sigma\mathbf{b}\cdot\mathbf{y})p(nV_\mathrm{th},\mathbf{y},t)}$$

$$q = \left\langle e^{i\ell V + i\mathbf{k}^\mathrm{T}\mathbf{Y}}\right\rangle$$

$$= \int\frac{\mathrm{d}\ell}{2\pi}e^{-inV_\mathrm{th}\ell}\left(\mu - i\sigma\mathbf{b}^\mathrm{T}\nabla_\mathbf{k}\right)q(\ell,\mathbf{k},t)\big|_{\mathbf{k}=0}$$

moment generating function

$$\tilde P_n(s) = \int_0^\infty \mathrm{d}t\, e^{-st}P_n(t) = \mu(1 - i\epsilon\mathbf{b}^\mathrm{T}\nabla_\mathbf{k})\varphi(nV_\mathrm{th},\mathbf{k},s)\big|_{\mathbf{k}=0}$$

$$\varphi(v,\mathbf{k},s) = \int_0^\infty \mathrm{d}t\, e^{-st}\int \mathrm{d}^d y\, e^{i\mathbf{k}\cdot\mathbf{y}}p(v,\mathbf{y},t)$$

weak-noise perturbation theory: $\varphi = \varphi^{(0)} + \epsilon\varphi^{(1)} + \epsilon^2\varphi^{(2)} + \cdots$

Analytical results

n^{th}-order ISI density

$$P_n(t) = \frac{1}{2\langle T\rangle\sqrt{4\pi\epsilon^2 h^3(t)}}\exp\left[-\frac{(t-n\langle T\rangle)^2}{4\epsilon^2\langle T\rangle^2 h(t)}\right]\times\left\{\frac{\left[\left(n-\frac{t}{\langle T\rangle}\right)g(t) + 2h(t)\right]^2}{2h(t)} - \epsilon^2\left[g^2(t) - 2h(t)C(t)\right]\right\}$$

$$\langle T\rangle = V_\mathrm{th}/\mu \qquad g(t) = \frac{1}{\langle T\rangle}\int_0^t \mathrm{d}t' C(t') \qquad h(t) = \frac{1}{\langle T\rangle}\int_0^t \mathrm{d}t'\, g(t')$$

ISI cumulants

$$\kappa_{2,n} = 2\langle T\rangle^2\epsilon^2\left\{h_n + \epsilon^2\left[g_n^2 + C(n\langle T\rangle)h_n\right]\right\} \qquad g_n = g(n\langle T\rangle)$$

$$\kappa_{3,n} = 12\langle T\rangle^3\epsilon^4 g_n h_n, \qquad h_n = h(n\langle T\rangle)$$

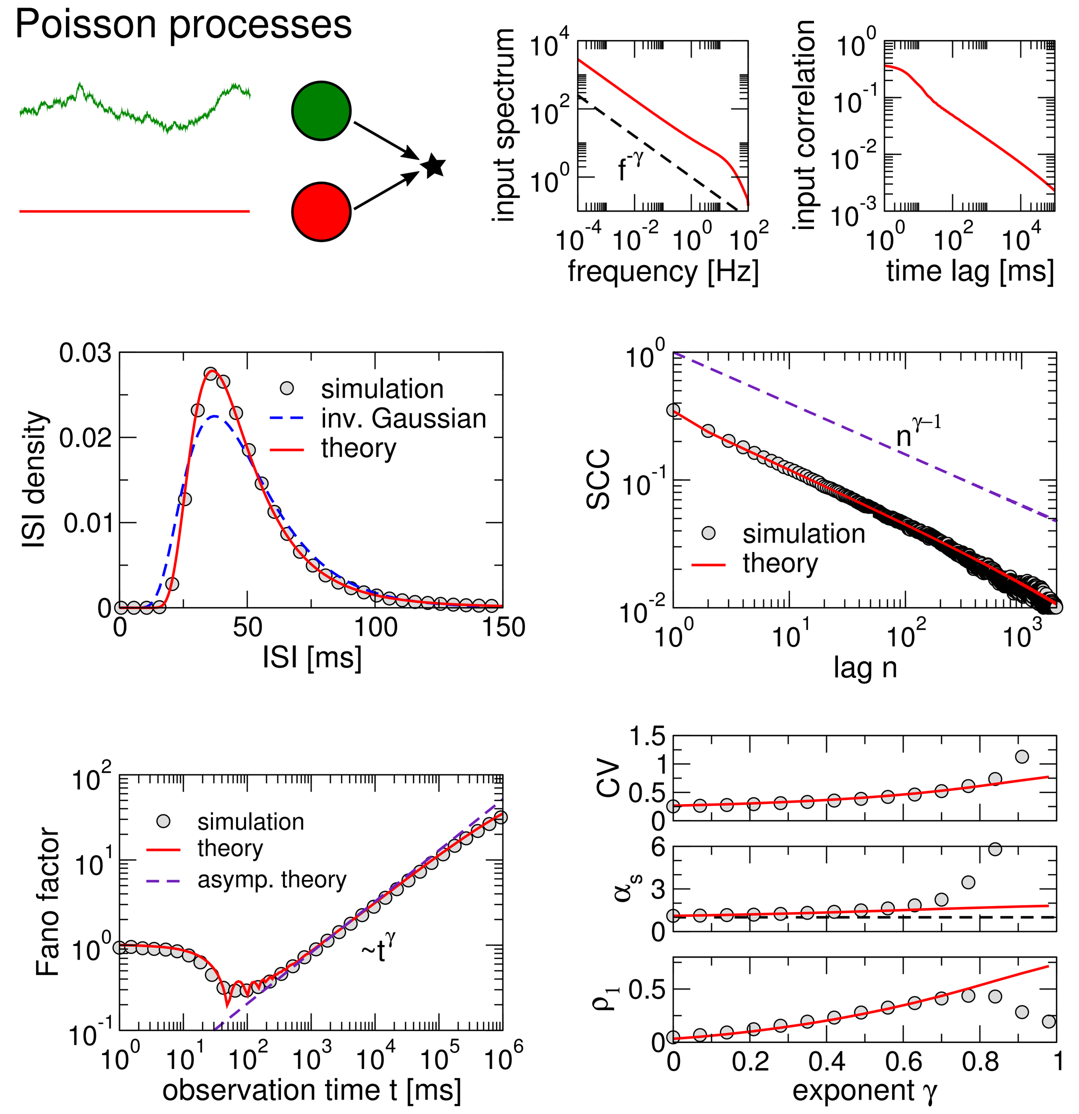
CV, skewness and ISI serial correlations

$$C_\mathrm{V}^2 \approx 2\epsilon^2 h(\langle T\rangle) = \epsilon^2\int \mathrm{d}f\,\tilde C(f)\mathrm{sinc}^2(f\langle T\rangle) \qquad \mathrm{sinc}(x) = \frac{\sin(\pi x)}{\pi x}$$

$$\alpha_\mathrm{s} \approx \frac{g(\langle T\rangle)}{h(\langle T\rangle)} = \frac{2\int \mathrm{d}f\,\tilde C(f)\mathrm{sinc}(2f\langle T\rangle)}{\int \mathrm{d}f\,\tilde C(f)\mathrm{sinc}^2(f\langle T\rangle)}.$$

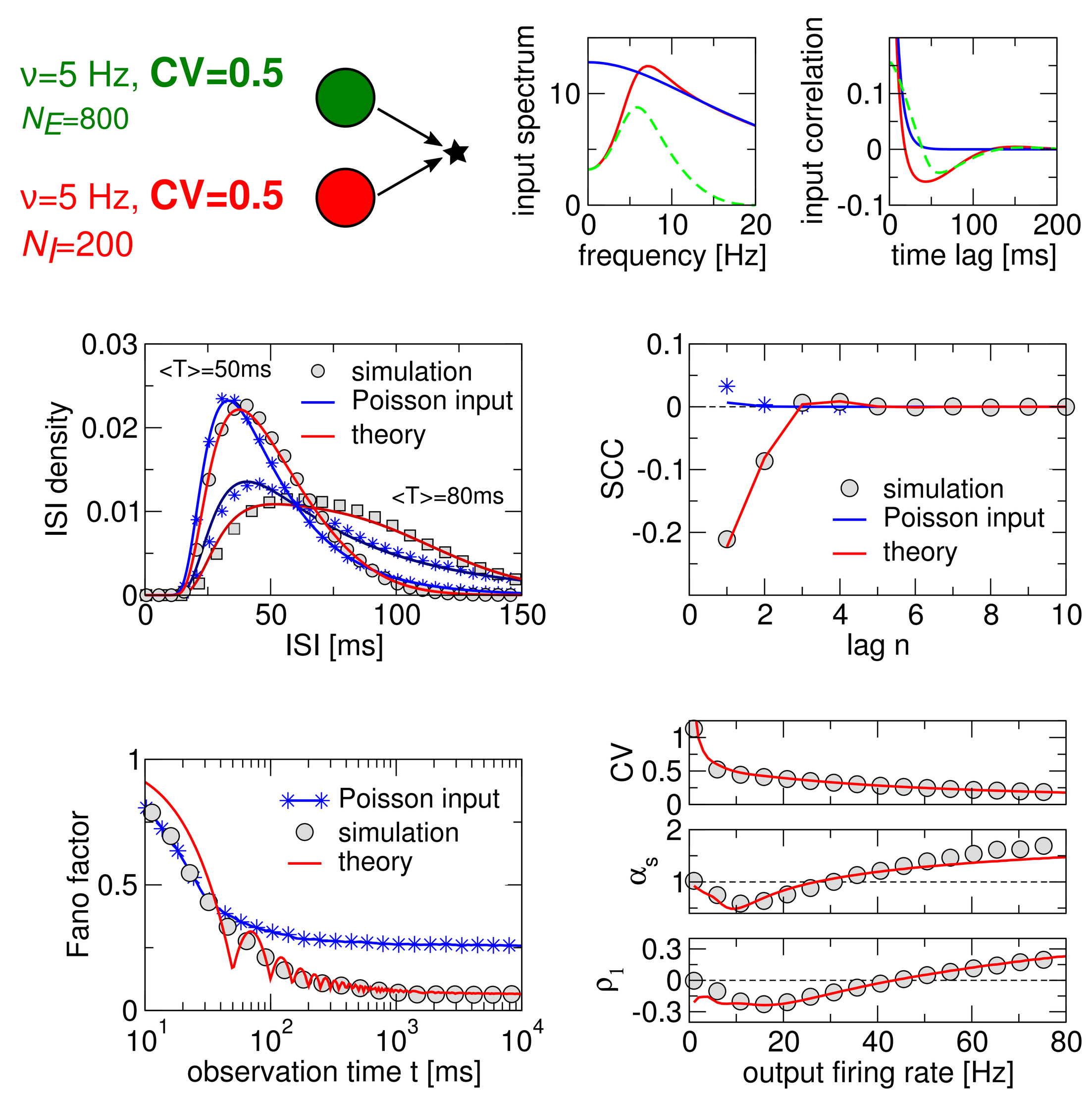
$$\rho_n = \frac{\kappa_{2,n+1} - 2\kappa_{2,n} + \kappa_{2,n-1}}{2\kappa_{2,1}} \approx \frac{\int \mathrm{d}f\,\tilde C(f)\mathrm{sinc}^2(f\langle T\rangle)e^{-2\pi i f\langle T\rangle n}}{\int \mathrm{d}f\,\tilde C(f)\mathrm{sinc}^2(f\langle T\rangle)}$$

Powerlaw input

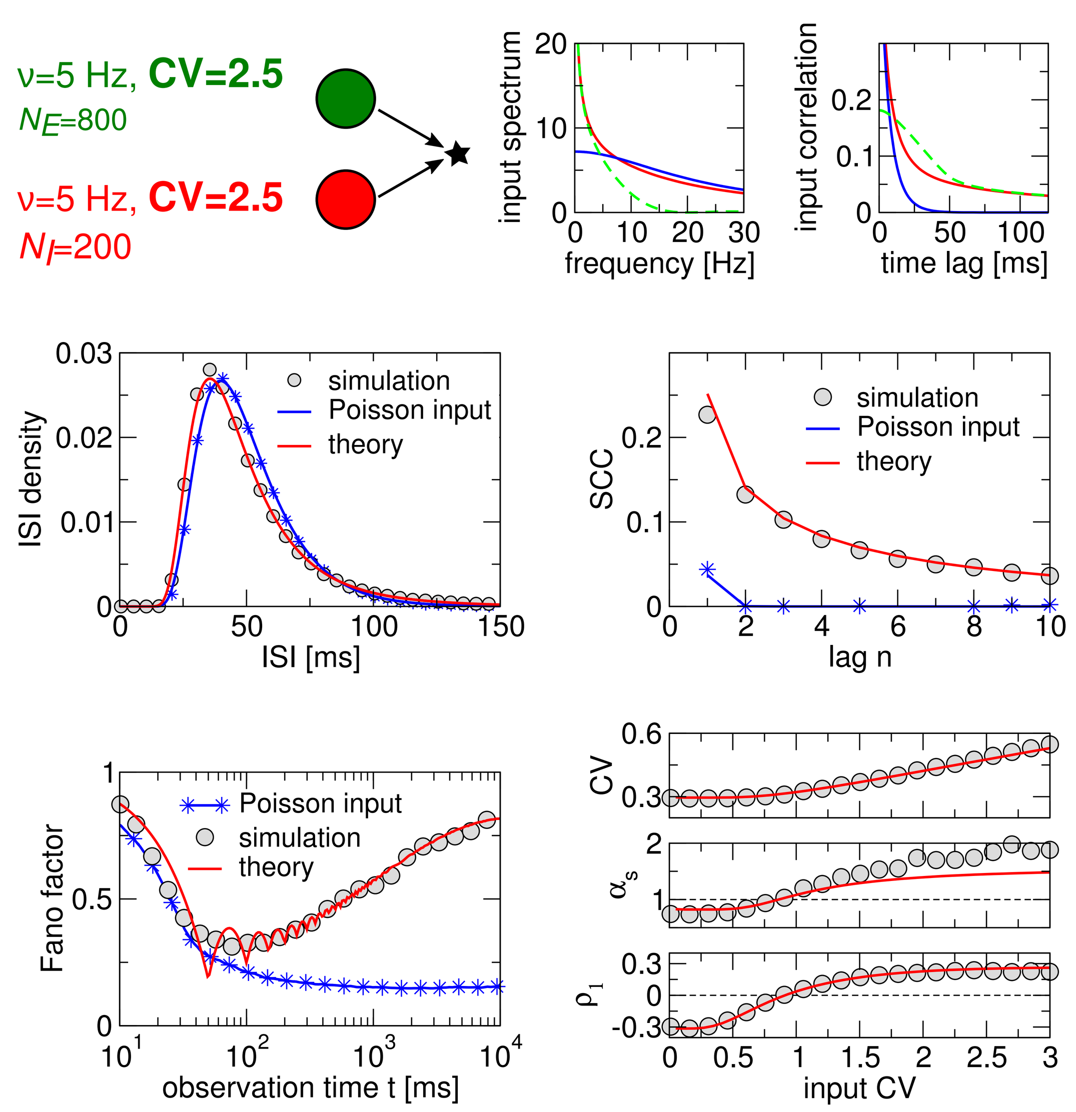


Non-Poissonian input

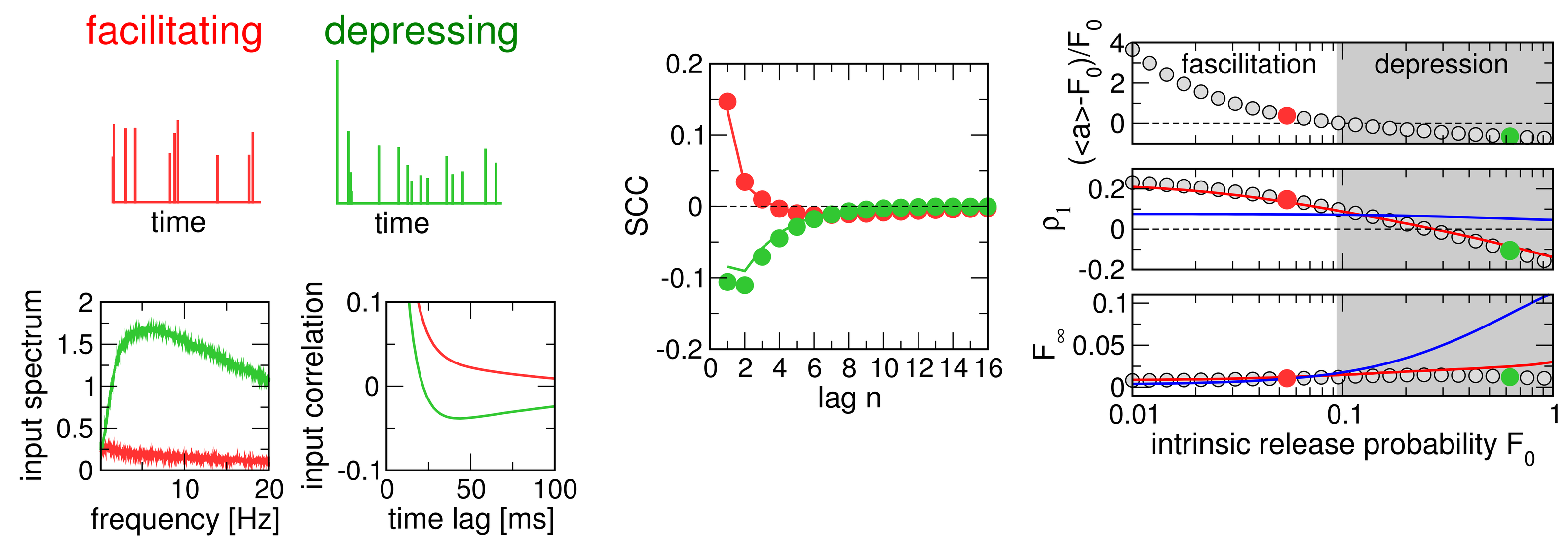
regular input spikes (refractoriness)



irregular input spikes (burstiness)



Short-term synaptic plasticity



Conclusions

- For Gaussian input with arbitrary correlation function, we derived analytical formulas for ISI density, auto-correlogram, CV, skewness, ISI serial correlations and Fano factor.
- works well for mean-driven regime with CV~0.5 or smaller
- regular input or synaptic depression => negative ISI correlations, small skew
- irregular input or facilitation => positive ISI correlations, large skew
- scaling behaviors for powerlaw input

Bauermeister C., Schwalger T., Russell D.F., Neiman A.B., Lindner B., PLoS Comp. Biol. 2013
Lindner B., Phys. Rev. E 2004